THE ALIMENTARY CANAL OF A CARBONIFEROUS SALAMANDER

DR. ROY L. MOODIE
THE UNIVERSITY OF KANSAS

INVESTIGATORS, during the progress of their research into the anatomy of extinct animals, have the good fortune, from time to time, to be able to add items of interest to the soft anatomy of the forms which they are studying. In the nature of the case the soft parts are very rarely preserved and when they are represented it is usually an imperfect record. Occasionally, however, the rocks yield forms which afford very complete knowledge of the soft anatomy of the animal. This has been strikingly shown in Dr. Dean's studies on the fossil sharks of the Cleveland shales of Ohio. Dr. Eastman and Dr. Parker have also studied and described the soft parts of the head, especially, of a peculiar little fish from the Waverly shales of Kentucky which Dr. Eastman has named *Rhadinichthys deani*. In this species, which is represented by an abundance of material, there are clearly preserved the various portions of the internal ear, the outlines of the lobes of the brain and traces of an arterial blood vessel with some of its branches. There are many other instances in which the soft anatomy of fossil fishes has been developed. Many of these are given more at length by the writer in another place.

Among the higher vertebrates the softer structures are not so well known. The outlines of various branchiosaurians are known from the studies of Fritsch, Credner, von Ammon, von Meyer and Thevenin, who have described these forms from the Permian and Carboniferous of France, Bohemia and Germany. Cope has dwelt at some length upon the preservation of the shape and some of the coloring matter of the eye of the reptile-

like microsaurian, *Amphibamus grandiceps,* from the Mazon Creek shales of Illinois. The writer has been fortunate in observing the outline of the body of this species. He has also observed muscle fibers in the abdominal wall and the outline of the body in *Tuditanus walcotti* from the Coal Measures of Ohio. He has described, also, the fin membranes, the lateral line organs, the form of the body and the "pigmentum nigrum" of the eye of *Micrerpeton caudatum* from the Mazon Creek shales. Dollo has described an unusual amphibian from the Wealden of Bernissart, Belgium, *Hylæobatrachus croyii,* which showed the preservation of some of the body membranes and thus a portion of the form of the body. Numerous observers have written on the form of the feet in amphibia as they have been recorded by their footprints in the rocks.

Nothing has ever been contributed to the structure of the intestinal tract of the fossil amphibia, and from the nature of the case as well as from the extreme rarity of approximately complete specimens of these animals it would be an unexpected event if such were discovered. Our confidence in the preserving powers of the rocks grows, however, from year to year, and if we look long enough we can not fail to uncover many things of interest.

The amphibia of the Mazon Creek shales have always been noted for the unusual perfection of their preservation, which they have shared with other animals and with the plants from that historic locality. *Amphibamus grandiceps,* the first amphibian described from these shales, was made known in 1865 by Professor Cope from an almost perfect specimen. The next species made known from these shales was the form described in 1909 by the writer under the name *Micrerpeton caudatum.* It was based on a specimen which lacked only portions of the limbs of being complete. Nothing of the intestinal tract was observed in either of these species. It was somewhat surprising, on that account, to observe among

a lot of specimens loaned the writer for study by Yale Museum, on two excellently preserved examples of the Branchiosauria, apparently adult, molds and impressions of what appeared at first sight to be intestines. Further study showed that in the smaller specimen there was preserved the *entire* alimentary canal and the other specimen had the alimentary tract approximately complete. There are no traces of branchiæ to be observed in either specimen.

The species which these forms represent is unknown and the writer has accordingly proposed for them, in another place, the name *Eumicrerpeton parvum,* new genus and species, and has regarded them as representatives of the family Branchiosauridæ. The smaller specimen has the more completely preserved canal of the two and the description given below will apply mainly to that specimen.

The nodule which contains this interesting little fossil measures two and a quarter inches by two inches and the fossil salamander occurs as nearly as possible in the center of the nodule (Fig. 4). The white kaolin which has usually replaced the bones in the Mazon Creek fossils has nearly all become eroded, only that of the right humerus remaining. The animal is of course preserved on its back.

If it were not for the fact that the œsophagus became loosened and dropped down from its place shortly after death, the alimentary canal would be in place and would immediately recall a freshly dissected specimen of a recent salamander. The anterior end of the œsophagus lies obliquely across the chest region with its tip pointing slightly downward. The length of the œsophagus proper is only about three millimeters. The entire animal measures but thirty millimeters in full length from the snout to the tip of the tail, the form of which is clearly preserved (Fig. 1).

The œsophagus, as it is preserved, lies in a semi-sigmoid curve with the convexity anterior. It enters the

cardiac portion of the stomach by a gradual constriction. The stomach is clearly preserved as a distinct sac-like organ with two lobes which correspond to the cardiac and pyloric limbs. The stomach measures about seven millimeters in length by two millimeters in its greatest diam-

FIG. 1. An enlarged photograph of the smaller specimen of *Eumicrerpeton parvum* showing nearly the complete course of the intestine. ×2.

eter. The muscular constriction which divides the organ into pyloric and cardiac divisions occurs at a distance of four millimeters from the upper end. The pyloris is designated by a rather pronounced constriction which may be partly accidental although it recalls the pyloris of the frogs very strongly. From this constriction, which lies on the left side of the fossil, as it is preserved, the duodenal portion of the intestine makes a straight course posteriorly to near the anal region, where it takes a sharp bend and curves back to run parallel with itself for the

distance of four millimeters. In its upward course, immediately on leaving the anal region, the intestine enlarges and practically the same enlargement continues throughout the remainder of its course to the anus. At the distance of a millimeter from the anal end the rectum dilates probably an eighth of a millimeter to form the

FIG. 2. An enlarged photograph of the larger specimen of *Eumicrerpeton parvum* showing portions of the impressions of the alimentary canal. × 2.

cloaca. After the intestine has continued its parallel course for the four millimeters as stated above, it turns abruptly to the right for a distance of two millimeters. It then runs posteriorly for a short distance, then bends back and under itself to again make a double sigmoid curve, when at a distance of six millimeters from the anus it assumes a straight course which it continues to the end (Fig. 3).

The anus lies at a level which is approximately that

of the lower end of the femur, which is preserved as an impression on the left side of the fossil, thus agreeing in its position with that found in the modern Caudata. Lying inside of the curve of the stomach and partly inclosed by the œsophagus is a smooth area which may

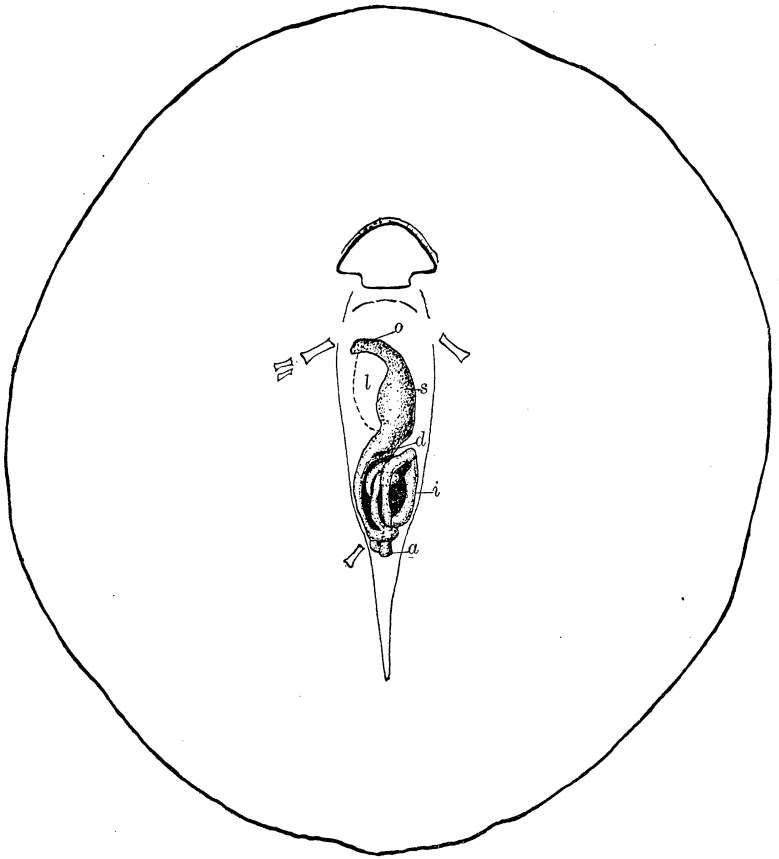

FIG. 3. A drawing of the smaller specimen of *Eumicrerpeton parvum* showing the full course and condition of the intestinal tract. ×2. *o*, œsophagus; *l*, liver; *s*, stomach; *d*, pyloris; *i*, small intestine; *a*, anus. Portions of the limb bones are also outlined as well as the anterior end of the interclavicle.

possibly represent the impression of some of the accessory digestive glands such as the liver. Occurring in this smooth area are numerous fine lines which possibly represent blood vessels; but they are so imperfectly preserved that I will not be sure.

The other and larger specimen (Fig. 2) is some ten millimeters longer than the example described above. The alimentary canal is represented not as a mold, as in the specimen described above, but by an impression from which the mold has been lost. By taking a wax impression of this specimen the form of the œsophagus, stomach and portions of the intestines, with the same form and arrangement as has been described, are beautifully shown. The œsophagus has also in this specimen been loosened and dropped down. The anus is quite prom-

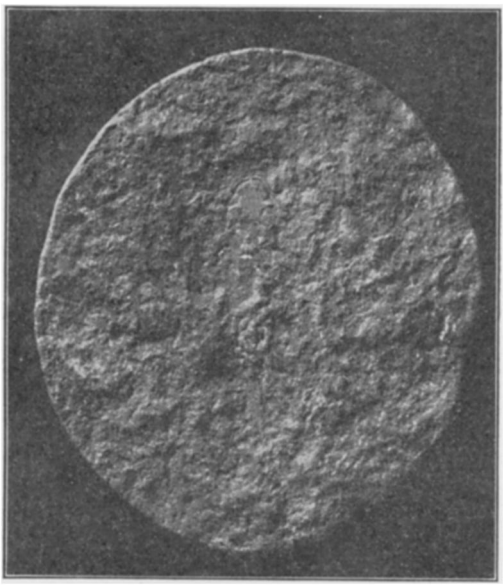

FIG. 4. The nodule containing the smaller fossil shown natural size.

inent and lies somewhat beyond the base of the tail. The tail is preserved entire in an elongate V. On its membranes are to be seen very clearly preserved the median and dorsal lateral lines which have been so completely described for *Micrerpeton caudatum*. Lying beside the anus in both specimens is a small elevation which may in both cases be accidental or it may represent either the posterior end of an oviduct or some anal gland which the branchiosaurians possessed.

The modern amphibia present many problems for consideration. Among the most interesting of these is the one which is concerned with the phylogeny of the living forms. An attempt has previously been made by the writer[1] to elucidate the problem of descent so far as the Caudata are concerned. The present contribution is a further extension of that effort and it supports the conclusions there drawn.

Representatives of several genera of the modern Caudata have been dissected in order to make a direct comparison of the fossil alimentary canal with that of the recent forms. Among the forms dissected may be mentioned *Ambystoma tigrinum, Ambystoma opacum, Diemyctylus torosus, Diemyctylus viridescens, Desmognathus fuscus* Raf., *Spelerpes bilineatus* Green, etc. In some cases representatives of several stages in the growth of the individual species have been available for study. The alimentary tract of *Desmognathus fuscus* Raf. from the vicinity of Ithaca, New York, resembles in a marked degree that of the fossil form. The nearest approach to the condition there represented is, however, found in an immature branchiate individual of some 47 millimeters in length, of *Diemyctylus torosus* Esch., from a fresh-water pond on Orcas Island in Puget Sound. The presence of this species on the island is very suggestive and its bearing on the geological age of the caudate amphibia will be given elsewhere. It is of extreme interest that the condition represented by the fossil should resemble so closely that of an immature rather than a mature form since it lends support to the recapitulation theory. Perhaps the representative species of the genera *Desmognathus, Spelerpes, Hemidactylus*, etc., are forms which have become restricted in their development and thus represent more nearly in the structure of their alimentary canal the ancestral condition, as is also the case in the immature form of the *Diemyctylus torosus* Esch.

The writer has attempted to show that the modern

[1] AMERICAN NATURALIST, XLII, No. 498, June, 1908.

Caudata are forms which have evolved by a process of degenerative evolution and he has supported his contention by a direct comparison of the skeletal anatomy of the Branchiosauria and the Caudata. So far as the skeleton is concerned the caudate organization is less high than that of the Branchiosauria. Such can not be said of the alimentary canal, for it at least has progressed in its development in many forms, although, as has been stated above, some of the more slender species are apparently restricted in their development. The fact that a young form of *Diemyctylus torosus* shows a closer approach to the fossil condition than any other is of extreme interest. It can be said with certainty that the *Diemyctylus torosus* goes through the phylogenetic stages in the development of its alimentary canal and in my opinion we have here a representative in the fossil condition of one of these phylogenetic stages. But too much importance can easily be attached to the close resemblances outlined above. It is to be remembered in this connection that the form of the alimentary canal is so highly modified by the food habits and by the form of the body of the individual animal that it will be difficult to draw safe conclusions. On the other hand, so far as we have ascertained, the form of the body of the salamanders has not changed essentially from that of their forebears, the Branchiosauria, so there is no really good reason why the form of the alimentary canal should have undergone much change.